WHISTLE DIALECTS OF THE ATLANTIC BOTTLENOSED DOLPHIN, *Tursiops truncatus*

By

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Abstract of Dissertation Presented to the Graduate Council of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

WHISTLE DIALECTS OF THE ATLANTIC BOTTLENOSED DOLPHIN, *Tursiops truncatus*

By

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Whistles of Atlantic bottlenosed dolphins, *Tursiops truncatus*, were investigated in an attempt to provide evidence for the utilization of dialects by this species. A total population of 158 dolphins, recorded at commercial aquaria and in the natural environment, was obtained for this project. The whistles of these animals were analyzed using both a spectrographic and an "audio-visual" technique. Thirteen different whistle parameters were measured for each animal. Subpopulations of dolphins were formed using the following characteristics: sex, age, sex-age class, area and region of origin (based primarily on water current patterns) and within-region sex and age classes. All whistle parameter measurements were subjected to statistical analysis and levels of correct identifications were computed. As a by-product of this analysis, mean values were computed for

all the whistle parameters. These values were then compared with the whistle parameter data found by earlier investigators in order to determine if any sizeable discrepancy exists among the various investigations. In addition, a captive bottlenosed dolphin was trained and utilized as a discriminator of whistle dialects.

The mean values obtained for the whistle parameters utilized in this study were found to be very similar to those reported in the research literature. No sex- or age-related whistle differences were found to exist when the total dolphin population was examined. However, a slight indication of sex-age class whistle differences was found. Area-related dialects were not found when the whistles of dolphins originating in waters off the Atlantic coast of Florida were compared to those of animals from the Gulf Coast. An identical type of discrimination was performed by the dolphin subject and, here again, no area-related dialects were found.

There was considerable evidence, however, that regional whistle dialects were utilized by these animals in Florida waters and that these whistle dialects were sex-related. Moreover, there was evidence for the presence of sex, age and sex-age class whistle differences within these regions. No single whistle parameter or set of parameters proved to be

responsible for the dialectical differences ascertained for the various regional subpopulations examined. It appears that a multiple set of whistle parameters was necessary to identify dialects and this set differed for each of the subpopulation discriminations. This finding lends support to the theory that each regional dolphin population develops its own whistle dislect independent of any influence from neighboring populations. It probably was the isolation of ecologically well-adapted dolphin groups that resulted in the whistle differences. Presently, there are insufficient data available to delineate the exact geographic ranges of dolphins that utilize particular dialects.

CHAPTER I

INTRODUCTION

A topic not often researched, but one of importance to the field of biocommunications, is that of the study of dialects within the calls of mammalian species. Indeed, in mammalian species other than man, the utilization of dialects has been verified only in the elephant seal, *Mirounga angustirostris* (LeBoeuf & Petrinovich, 1974). The lack of research in this area may be due to the large amounts of gradation and acoustic complexity within the repertoires of most mammalian species, particularly those of higher primates (LeBoeuf & Peterson, 1969). Nevertheless, it appears to be an area of potentially fruitful study, especially when the species' call is one which can be easily identified and analyzed.

Dialects: A General Description

The term dialects refers to consistent differences in the songs or calls of neighboring populations of a particular

species or between populations with individuals which have the potential for interbreeding (Nottebohm, 1969). Dialects have been found to exist in the calls of insects (Dumortier, 1963), amphibians (Capranica, Frishkopf & Nevo, 1973) and birds (Marler & Tamura, 1964; Nottebohm, 1969; Lemon, 1971; Milligan & Verner, 1971 et al.). Substantial study has been carried out on the dialectical behaviors of many subspecies within these classes. It is argued that for dialects to be formed, at least the following three conditions must be present: (1) some isolation of the population (either through behavioral differences or geographic barriers), (2) a means of transmitting the song or call from generation to generation, and (3) sources of variation within the song so that individuals of a species residing in different areas may diverge in the use of differing song types (Lemon, 1966).

Function of Dialects

It is theorized that dialects may have developed so as to discourage the intermixing of subpopulations of a species that have adapted to local ecological conditions (Nottebohm, 1969). In order for dialects to function as population markers, an individual must acquire the dialect while still living near its place of birth and in the company of members

of its own subpopulation (Nottebohm, 1970). Marler and Hamilton (1968) argued that dialects may aid in distinguishing between subpopulations and function as a guide to permit lost individuals to rejoin their particular group. Conversely, these same authors present the possibility that dialects may have no direct communicative function, but rather develop to fulfill some other biological need of the species. Nevertheless, it is quite possible that dialects aid in achieving a compromise between maximum environmental adaptation and maintenance of ecological flexibility (Orejuela & Morton, 1975). There appears to be some question regarding whether dialects induce isolation of subpopulations or if the formation of dialects is the result of this isolation (Nottebohm, 1969). In any event, the song dialect of a subpopulation serves to reinforce the isolation between neighboring groups and this isolation has the potential to increase the probability of genetic differences arising between subpopulations (Lemon, 1966). The strength of a dialect (as an isolating mechanism) appears to be greatest when a subpopulation is not facing extinction and, if the possibility of species extinction emerges, the isolating effects of the dialect probably would be greatly reduced (Nottebohm, 1969).

Dialects in Birds

The dialects of avian species have received more attention than those of any other class of animal. This occurrence is perhaps due, at least in part, to the manageable analysis of bird song, the relative ease of working with birds under both field and laboratory conditions and the broad base of available knowledge regarding the geographic ranges and natural histories of avian species. It is not known if any meaningful analogies can be made between avian and mammalian dialects; however, the potential use of this knowledge must be investigated. The paucity of information regarding the dialects of other classes of animals precludes the use of comparisons between these dialects and those of mammals. In any case, the nature and study of the dialects in bird song can serve as a reasonable model for similar study of the calls of mammals. Accordingly, this area will be reviewed as a prelude to the research undertaken in this project.

The Nature of Bird Song

Singing constitutes a large portion of the behavioral repertoire of many avian species. Such activity is usually

associated with the possession of particular territories by subpopulations of a species (Harris & Lemon, 1972) and is most often produced by males during mating seasons (Mundinger, 1975). Further, as Marler (1956) suggests, bird song also may serve to communicate a great deal of information about the emitter to other individuals. Such information could include its species, sex, location, individual identity, motivation and breeding status. Each specific class of information sent must be conveyed by an optimal signal form and there is evidence to suggest that these signals are different for each variety of message used by birds (Emlen, 1972).

Composition and Development of Bird Song

In order to reasonably understand the use and evolution of avian dialects, a knowledge of bird song development would appear necessary. Bird song can be divided into segments (called syllables) which consist of from one to three sound units (Lemon, 1975); these syllables are repeated in groups called utterances. The term "song type" refers to the variety and sequence of syllables used in an utterance.

Nottebohm (1971) divided the development of chaffinch song, during the first year of its life, into the following stages: (1) Subsong--a loose accumulation of low amplitude notes displaying a variety of complexity; (2) Plastic song--an intermediate stage composed of passages of highly variable song mixed with the subsong. Such variability, during this period decreases over time and the song becomes stereotyped: (3) Full song--this call constitutes the final stage of song development. That is, at this point, the song has become "crystallized" into a stereotyped form which retains its theme, with only minor variations, over the course of years.

Formation and Variety of Avian Dialects

In order to understand the use of dialects by birds, it is helpful to study the method by which dialects are formed and the varieties of dialects in use. In some bird species, the song is well formed at birth and individuals of these species exhibit little variation in their song patterns even when they inhabit a geographically distinct region. Other bird species, however, have only a rough framework of a song at birth and apparently learn the fine structure of the song by imitation. Species exhibiting this latter type

behavior are often found to develop measurable dialects (Frings & Frings, 1964). For example, Marler and Tamura (1964) reported that male white-crowned sparrows, Zonotrichia leucophrys, learn song dialects from other males during the first one hundred days of life and, during this period, can successfully be taught an "alien" dialect (of its own species, of course), in a laboratory environment. However, the dialect of other avian species are not copied and, once the song is developed, it remains unchanged. There appears to be no need for a social bond between the infant bird and the bird whose signal is copied. Lemon (1974) utilized playbacks of recorded cardinal (Cardinalis cardinalis) dialects to elicit responses from other cardinals. It was found that songs of individuals from distant regions brought about a lower response (measured by the number of reply songs evoked and the number of approaches toward the sound source) than did local songs. Song sparrows, Melopsiza melodia, have also exhibited an ability to discriminate between local and alien dialects (Harris & Lemon, 1974).

Harris and Lemon (1972) summarized the nature of avian dialects as follows: (1) each individual sings a single song pattern and only a small amount of variability exists among the birds within the same subpopulation, (2) each

individual exhibits a repertoire of different song patterns with identical patterns being used by the majority of individuals in that population, and (3) each individual has a repertoire of song patterns of intermediate variability. Dialects have not been found in all avian species and species vary in the amount of song conformity within a population.

The Atlantic Bottlenosed Dolphin

Having explored the presence of dialects in birds, a case now may be developed for the presence of such dialects in the whistle mode of the Atlantic bottlenosed dolphin.

Natural History

The study of the natural history of a species is necessary to help establish the possible need for dialects within subpopulations of that species. Such information is necessary, because much of the function of dialects deals with the relationship of a population with its environment. *Tursiops truncatus*, the Atlantic bottlenosed dolphin, appears to be a good experimental subject for the study of mammalian dialects. It is the most common inshore species of the cetacean order within the state of Florida (Moore, 1953) and inhabits bays, lagoons and large rivers (Caldwell & Caldwell, 1972a).

Usually, T. truncatus is seen assembled into small herds of from two to over ten individuals, however, groups with as many as 100-500 members have been observed (Nishiwaki, 1972). Dolphin family groups almost always consist of a single adult male, three to five adult females and a variable number of infants; usually up to two years of age (McBride & Kritzler, 1951; Caldwell & Caldwell, 1972a). In addition, homogeneous units of male animals have also been reported (True, 1891; Irvine & Wells, 1972). These may be quite stable except during the mating season when there is an apparent mixing of sexually segregated populations for short periods of time (Robinson, 1973). Slijper (1962) noted that mutual ties are very close within herds of ceteceans and these ties appear to be maintained principally by the use of emitted calls. Thus, it appears that should a dialect exist within this species, it might function as a means of reuniting sexually segregated groups and maintaining relationships within individual herds.

Distribution and Migrations of Bottlenosed Dolphins

To illustrate the presence of dialects between subpopulations of a species, some evidence of isolation of these groupings must be observable. Presently there is little evidence

for long distance migrations of Tursiops truncatus in Florida coastal waters (Migaki et al., 1971). The observed migratory range of this species appears to be from fifty to one hundred miles parallel to the shoreline and they may range from fifty to one hundred miles seaward (Caldwell & Caldwell, 1972a). It appears that Florida Atlantic bottlenosed dolphins form resident habitats (Moore, 1953; Caldwell, 1955; Caldwell et al., 1971; Irvine & Wells, 1972) and even maintain micro-territories within these habitats (Caldwell & Caldwell, 1972a). This conclusion is based upon observations of tagged dolphins (e.g., via individual physical peculiarities and artificial tags).

Important among the factors delineating the distribution of this species is food supply. Therefore, one possible reason for bottlenosed dolphin migrations could be the seasonal movements of food species (Essapian, 1962). It has recently been reported, however, that the bottlenosed dolphin, in Florida, is relatively plastic in regard to food habits and, therefore, is not dependent on following the movements of its food supply for survival (Leatherwood, 1975). Another limitation to lengthy migrations by a species would be obstructing physical boundaries. In this regard, the coastal waters of Florida can be divided into zones based upon water

circulation patterns (Jones, O'Brien & Hsueh, 1973; Austin & Jones, 1974) and these discrete oceanic currents could serve as discernible potential barriers to migrations. The role of water currents as boundaries to cetacean migrations has been established (Miyazaki, Kasuya & Nishiwaki, 1974; Nasu, 1974). However, it is possible that the influence of these currents can be correlated with the thermal variations, which function as an influence on the movements of food fish species (Norris, 1967).

The Whistle of the Bottlenosed Dolphin

Since the major focus of this study is upon the dolphin whistle and its potential dialects, it appears appropriate to describe the nature and function of this call. Basically, bottlenosed dolphins produce two major types of sounds: broad band clicks and whistles (Wood, 1953). The clicks appear to be used primarily for environmental investigation and for food finding (Kellogg, 1961). Dolphin whistles have been defined as narrow band phonations usually exhibiting changes in frequency (Schevill & Watkins, 1962). Kellogg, Kohler and Norris (1953) have reported that dolphin whistles usually are initiated at about 7 kHz, peak at about 15 kHz and have a duration of approximately 0.5 seconds. Slightly

varying descriptions have been published by other researchers (Dreher, 1961; Lilly & Miller, 1961a; Evans & Prescott, 1962; Dreher & Evans, 1964). All of these descriptions, however, are based upon very small populations so that no single description of the whistle can be said to represent even a reasonable sample within the entire species. Finally, the dolphin whistle differs from bird song primarily in its lack of complexity and the absence of the easily recognizable syllables found in bird song (Caldwell & Caldwell, 1970).

Possible Functions of the Dolphin Whistle

Over the past thirty years, there has been much controversy regarding the utilization of whistles by dolphins. A number of theories relative to this issue have been proposed. An understanding of these theories would appear important since they may demonstrate or refute the presence of dialects within this species. The theory that dolphin whistles possess communicative value was first proposed by McBride (1940). It was later noted that captive dolphins produced varied whistles under different behavioral conditions and in different environments (Wood, 1953). On this basis, Lilly (1961) developed a hypothesis which

attempted to assign specific whistle contours to particular behavioral situations and to establish the existence of a dolphin language. Lilly's postulations have not been supported by experimental evidence and further work in this area (Dreher, 1966) is of questionable validity.

Another relationship should be noted. Solitary dolphins have been observed to produce whistles less frequently than dolphins residing in groups (Lilly & Miller, 1961b). This behavior is perhaps due to a lack of response from the environment and especially from other dolphins. It also has been noted, however, that as the size of a dolphin herd increases, the number of phonations expands geometrically rather than arithmetically (Caldwell & Caldwell, 1966) and observations such as these have led to the formation of the theory of the probable social functions of the dolphin whistle (Caldwell & Caldwell, 1972b). These social functions may be to alert other dolphins to the presence of an individual, identify that individual to other herd members, provide the location of the individual and perhaps give an indication of the individual's emotional state.

It is possible that, at present, the most widely accepted whistle theory is that of the "signature" whistle. Essapian (1953) observed that individual dolphins may have distinctive

calls that other dolphins can recognize. He based this theory upon the fact that an infant dolphin responds to its mother's call and the mother to the infant's call; further, female dolphins may be found to answer the calls of a particular male. In any case, the whistle of the bottlenosed dolphin is present at birth, but in a rough form which appears to become more developed as the animal matures (Caldwell & Caldwell, 1972b). The mother dolphin begins whistling as soon as the infant is born and each soon learns to recognize the whistle of the other (Caldwell & Caldwell, 1967). An infant dolphin separated from its mother whistles almost constantly until reunited (Wood, 1953).

The actual formation of the signature whistle theory, i.e., one in which most of the whistles emitted by a dolphin are characteristic to that individual dolphin, was initiated by Caldwell and Caldwell (1965). Other researchers have since substantiated these findings (Powell, 1966; Titov et al., 1971). The signature whistle is described as being consistent in basic contour, but varying in: (1) the number of whistles produced per minute, (2) the intensity and duration of each individual whistle, and (3) the nature of the whistle breakoff and quaver (Caldwell, Caldwell & Miller, 1973). The greatest changes occur in the dolphin whistle

when the animals are exposed to fear-inducing situations which usually result in tremulous, frequency limited and partial whistles (Caldwell & Caldwell, 1972c). Some dolphins have a tendency to vary their basic whistle contours but apparently they do so infrequently (Caldwell & Caldwell, 1966). In general, the signature whistle makes up from 90 to 100 per cent of a typical dolphin's whistle repertoire (Caldwell & Caldwell, 1968).

Testing the Signature Whistle Theory

It has been demonstrated that a captive bottlenosed dolphin can discriminate between conspecifics by means of recorded playbacks of their signature whistles and this discriminatory ability was not hampered by using test whistles representing both sexes (Caldwell, Caldwell & Hall, 1971). Further evidence to strengthen the signature whistle theory emerged with the findings that individuals from other cetacean species can be identified by means of their respective signature whistles. The basic theory has been tested on the following species: *Stenella plagiodon* (Caldwell, Caldwell & Miller, 1973), *Lagenorynchus obliquidens* (Caldwell & Caldwell, 1971) and *Delphinus delphis*

(Caldwell, Caldwell & Hall, 1973). To summarize, it appears that the Atlantic bottlenosed dolphin uses the signature whistle in an analog form of communication. Since the whistles are individual-specific, consistent similarities among the individuals of a population and consistent differences between geographic groups of individuals must be sought in an attempt to prove the existence of dialects in the species.

Dialects in Cetacean Species

As yet, no dialects have been demonstrated to exist in any cetacean species; however, there has been some speculation that they do exist. Essapian (1962) noted that placing a dolphin from the Gulf of Mexico into a tank housing three dolphins captured in Biscayne Bay resulted in an atmosphere of unfriendliness. Based on this observation, he speculated that differences in vocalizations could exist between dolphins living in different geographic areas. Moreover, Howard Winn (Anonymous, 1971) has proposed that dialects may exist in the call of the humpback whale, *Megaptera novaeangliae*, and it is possible that beluga whales, *Delphinapterus leucas*, residing in different geographical areas, also possess dialects (Morgan, 1973). Spotted dolphins,

Stenella attenuata, from two different localities reacted differently to sound playbacks, thus indicating that dialects may also exist in this species (Fish & Lingle, 1973).

Summary

From the above discussion, it appears likely that the Atlantic bottlenosed dolphin has a means of learning a dialect (i.e., the whistle) through imitation at an early stage in its life. These dolphins appear to exist in relatively isolated groups in specific geographic areas. This observation, in addition to the possibility of sexual segregation, offers some potential to the theory that regional and sex-related dialects exist for this species. The isolation of regional groups is probably enhanced by the water current boundaries. It should be noted, however, that these dolphins may have a large acoustic memory capable of storing discriminatory information necessary for identification of specific individuals via their signature whistles.

Purpose

The goals of this research project are to: (1) explore the possibility of population/regional dialects in the whistle mode of those Atlantic bottlenosed dolphins that reside

within the coastal waters of Florida, (2) examine the probability of age and sex-related whistle differences in this species, (3) explore the significance of a number of acoustic parameters in relation to dialects, and (4) assist in the delineation of the extent of dolphin territoriality and migration via the geographic range of individuals utilizing specific dialects.

CHAPTER II

PROCEDURE

In an effort to determine if bottlenosed dolphins residing in the coastal waters of Florida exhibit dialects in their whistle emissions, the following experimental plan was devised and implemented. First, a systematic accumulation of previously analyzed Tursiops truncatus whistles, representing ninety-seven animals captured or stranded within the state of Florida, was obtained from the tape library of Dr. and Mrs. David K. Caldwell. This set of materials will be referred to as the "library" recordings. They were analyzed acoustically for evidence of dialects. A similar analysis was carried out on a new corpus of recorded dolphin whistles obtained in the field. This second group of materials (they will be referred to as the "field" recordings) were gathered at commercial aquaria as well as in the natural environment and were based on the whistles of sixty-one additional dolphins. As stated, the whistle recordings obtained from this sample of 158 dolphins were used to explore the possibility that area-, region-, sex- and/or

age-related dialects exist within the Florida population of this species. In addition to the data analysis cited above, a dolphin subject was utilized in a whistle discrimination experiment designed to substantiate the existence of whistle dialects between dolphins residing in geographically distant areas.

Whistle Analysis Procedure

Recording Equipment

The "library" materials utilized in this research were taped on various models of Uher tape recorders and the "field" materials were taped on Uher Report L or Report IC tape recorders. When operated at a tape speed of 7.5 inches per second, the frequency response of these machines is uniform over the range 40 Hz to 20 kHz. An Atlantic Research Corporation LC-57 hydrophone was the primary transducer utilized to secure underwater phonations and a Uher hand-held microphone, associated with the recording unit, was used to collect the "in-air" vocalizations. All recording conditions (e.g. weather, time of day, etc.) and other observable subject behaviors were noted in a written log book. An effort was made to secure only recordings

within normative situations but whistles produced under stressful conditions also are represented within the population. In order for a subject to be included in this project, a minimum of ten recorded whistles was required.

The analyses of the whistles were carried out by two methods: a spectrographic analysis and an "audio-visual" analysis. The first of these two techniques utilizes the sound spectrograph. For the purposes of this study, a representative signature whistle was chosen for each subject and a time-by-frequency-by-amplitude spectrogram was made of the signal. The recordings (previously recorded at a speed of 7.5 inches per second) were reduced to half-speed when the spectrograms were made--by this means the frequency response of this device was increased by a factor of two (e.g., the frequency range of 80-8000 Hz was thusly increased to 160-16,000 Hz). All "library" recordings had been previously analyzed on a Kay Model 662A Sonagraph, however, they were remeasured to insure accuracy. The "field" recordings were processed on a Kay model 6061-B Sonagraph.

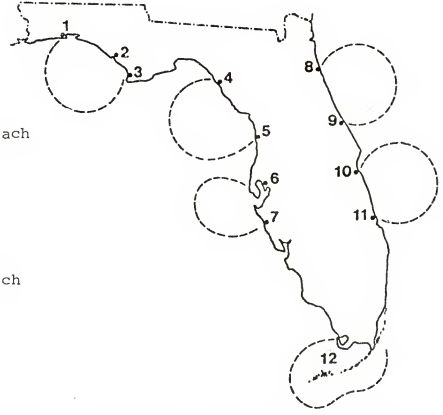
The "audio-visual" method consisted of slowing down the experimental tape recordings to 1/8th their normal speed, hand drawing the whistle contours heard by the human ear and timing the whistle durations with a stopwatch; these

temporal data were then converted back to real time. This procedure has been used both for the study of avian species (Marler, 1956) and cetacean species (Dreher, 1966). It is a technique that has been shown to exhibit whistle duration accuracy to within one-tenth of one second when measured against the sound spectrogram of that same whistle (Caldwell & Caldwell, 1971). An individual needs training and experience in order to achieve accurate whistle analysis using this method; the experimenter received such training during a one year traineeship at the Biocommunications facility of the Institute for the Advanced Study of Communication Processes located at Marineland, Florida. Two Uher Report L tape recorders were used for the "audio-visual" analysis.

Subject Classifications

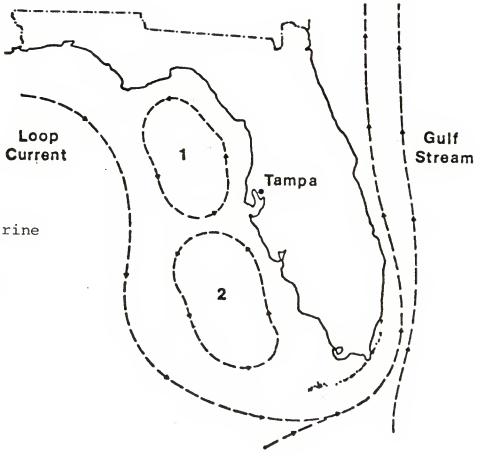
The following classifications were used to develop the dolphin subpopulations that would be subjected to individual analyses: (1) the sex of the dolphin, (2) age class (based upon Sergeant, Caldwell & Caldwell, 1973): Class 1 dolphins are juveniles ranging from 170 to 210 cm in standard length (measured in a straight line from tip of upper jaw to the notch in the center of the flukes). The Class 2 group were subadults consisting of dolphins that range from 210

to 235 cm in standard length in females and 247 cm in males. The Class 3 dolphins, or adults, were of greater standard length than were the subadults; these subjects were sexually mature, (3) area of origin: the two major areas chosen for investigation were the waters adjacent to the Gulf and Atlantic coasts of Florida, (4) regions of origin (see Figure 1) were based upon the distribution of major water current patterns (Figure 2) and the locations of the six largest population groups which could be formulated from the available data. Through personal observation and communication with knowledgable individuals, it was determined that large resident populations of dolphins reside in these regions. Further, it is possible that each of these regions encompassed several dolphin populations, however, the size of the population of recorded dolphins precluded any further breakdown of the regions. The following regional classifications were formed and utilized: the St. Augustine region (dolphins originating between New Smyrna Beach and St. Augustine), the Melbourne region (dolphins originating between Vero Beach and Melbourne), the Keys region (dolphins originating within the Florida Keys), the Tampa region (dolphins originating between Sarasota Bay and Tampa Bay), the Steinhatchee region (dolphins originating between Homasassa Bay and Steinhatchee) and the Destin region



1. Fort Walton Beach
2. Panama City
3. Port St. Joe
4. Steinhatchee
5. Homasassa Bay
6. Tampa Bay
7. Sarasota Bay
8. St. Augustine
9. New Smyrna Beach
10. Melbourne
11. Vero Beach
12. Florida Keys

Figure 1. The Six Regions of Dolphin Origin Utilized in This Study. The Destin Region Extends From #1 to #3, Steinhatchee Region From #4 to #5, Tampa Region From #6 to #7, St. Augustine Region From #8 to #9, Melbourne Region From #10 to #11 and the Keys Region is #12.



1. West Florida Estuarine Waters

2. Florida Bay Waters

Figure 2. Summer Water Current Patterns in the State of Florida Based on Austin and Jones (1974).

(dolphins originating between Port St. Joe and Fort Walton Beach). A breakdown of the total population into discrete classifications is presented in Table 1.

Whistle Parameters

The two analysis methods yielded a total of thirteen whistle parameters. Seven parameters were obtained from the spectrographic method and six from the "audio-visual" method. The selection of these particular parameters was influenced by the need for both temporal and frequency data and the requirement that the combination of parameters provide an accurate representation of the signature whistle of each dolphin. A description of each of these characteristics is presented below.

The following parameters were derived from the analysis of the spectrograms: (1) lowest observed frequency (in kHz), (2) highest observed frequency (in kHz), (3) frequency at onset of whistle (in kHz), (4) frequency modulation: the frequency difference between the high and low frequency extremes (in kHz), (5) frequency modulation in time: the amount of time (in seconds) needed for a frequency modulation, (6) loop duration: the amount of time (in seconds) necessary for the completion of a single loop (the term

Table 1. Breakdown of the Number of Dolphins Used in This Research and Their Reclassification into Sub-populations.

Group	Sample Size*
1. Total Population	158
2. Area	
Atlantic	74
Gulf	84
3. Sex by Area	
Atlantic Males	29
Gulf Males	40
Atlantic Females	43
Gulf Females	44
4. Sex	
Males	69
Females	87
5. Age	
Age Class One (Juveniles)	48
Age Class Two (Subadults)	61
Age Class Three (Adults)	46
6. Sex-Age	
Male Age Class One	28
Male Age Class Two	28
Male Age Class Three	12
Female Age Class One	20
Female Age Class Two	33
Female Age Class Three	34
7. Region	
St. Augustine	44
Melbourne	13
Keys	10
Tampa	22
Steinhatchee	32
Destin	25

*Total sample sizes for each categorical grouping may differ slightly from the total population sample size due to a lack of information concerning the sex and/or age of some animals. In addition, dolphins from regions with populations of less than ten individuals were not included.

loop refers to an entire production of a sound pattern cycle), (7) whistle duration: the amount of time (in seconds) necessary to produce an entire whistle (the samples examined were chosen so as to be the best representation of each dolphin's signature whistle). The parameters derived from the "audio-visual" method for each dolphin were: (1) loop duration (in seconds): this measure was obtained by dividing the mean whistle duration by the mean number of loops per whistle, (2) whistle duration: the mean amount of time (in seconds) necessary to produce an average whistle, (3) number of loops per whistle: this measure was derived by counting the total number of loops present in a series of whistle contours and then dividing this value by the total number of whistles, (4) maximum number of loops per whistle: the greatest number of loops counted in a whistle contour, (6) minimum whistle duration (in seconds).

Statistical Approach to Data Analysis

All data generated by this project were evaluated by the Stepwise Discriminant Analysis statistical procedure of the Biomedical Computer Program (BMD 07M). This procedure performs a multiple group discriminant analysis by computing a set of linear classification functions via the choosing

of independent variables in a stepwise form. In moving from one step to the next, a single variable is added or removed from the discriminating set. One of four available criteria are used to select the variable that is entered at each step. Variables are included when their F values are greater than .01 and deleted when their F values are too low for meaningful computation to continue (F value for deletion = .005). If a variable falls below the tolerance level (.0001), it is omitted from further computations. The probability of case misclassification or case correct classification can be computed by utilizing the results listed in the group classification table.

Dialect Discrimination Experiment

Another experiment was carried out in order to test the possibility that dialects exist in the whistles of the bottlenosed dolphin. In this experiment, a dolphin subject was used to discriminate between whistles of dolphins from northeastern and northwestern coastal areas of Florida. The subject was required to identify certain whistle stimuli by pressing an underwater paddle. A description of the experimental procedure is presented below.

Subject

The subject of this study was a subadult, male *T. truncatus* (MLF 232). This animal was captured near the mouth of the Suwannee River (Florida) in May, 1968. He had been subjected to a substantial amount of training and experimentation and had been isolated throughout most of his captive life. During this experiment, he was housed in a circular tank, 6.55 m in diameter and 1.83 m deep.

Apparatus

The whistle stimuli were presented underwater via a USRD type J-9 Audio Frequency Transducer coupled to a Uher Report 1C tape recorder (the operating range of the transducer is 40 to 20,000 Hz). An underwater paddle was utilized in this experiment. The arm of the paddle was constructed of plastic tubing and the paddle face was a wooden rectangle (2.5 x 3.5 cm) covered with foam rubber. The paddle was suspended 30 cm below the water line and 30 cm away from the tank wall. A wooden structure concealed the experimenter from the subject's view during the experiment. The use of this structure was necessary in order to prevent the presentation of any unintentional visual cues to the subject.

Preparation of the
Stimuli Tapes

Initially, a training tape was made which contained the whistles of dolphins originating in northeast Florida; no dolphins were used that were taken from waters south of New Smyrna Beach. This "positive" stimulus training tape consisted of twenty segments of four whistles each, representing twenty individual dolphins from this area. Subjects consisted of a variety of sexes and ages, with the exception that no infant whistles were used. None of these whistles were reused in the experimental test tapes. A second training tape was constructed which consisted of recordings of dolphin whistles produced by animals captured in northwest Florida waters and no animal that originated in the Gulf south of Yankeetown was used. The whistles from northwest Florida dolphins were established as "negative" stimuli. The negative stimulus training tape contained the whistles of fifteen individual dolphins in varied order--for a total duration of thirty minutes. The whistles of these dolphins were not reused in the experimental trials.

The experimental stimuli were carefully chosen so that no known extraneous cues were present in a given sample. Care, also, was taken to insure that the samples used were

representative of the signature whistle of each dolphin. Four experimental tapes were constructed. Each of these tapes consisted of twenty-five trials with four whistles from an individual dolphin constituting a trial. In all, the whistles of twenty-five dolphins from northeast Florida and twenty-five dolphins from northwest Florida were represented on these tapes and each dolphin's whistles were presented to the subject on two different occasions within the four experimental tapes (one hundred trials). A random order of northeast and northwest Florida dolphin whistles was used; the order of presentation of the experimental tapes also was random.

Experimental Procedure

In order to train the subject to associate the presentation of a positive stimulus with the pressing of the paddle, he was exposed only to positive stimuli and rewarded for all correct responses. Further, the subject was conditioned to "hold station" until a stimulus was presented via the underwater sound system. Upon cessation of the signal, a time period of ten seconds was permitted for the subject to make a response. For each correct response, the subject was rewarded with a piece of cut fish presented simultaneously with a single blast of a whistle. Incorrect

responses (failure to press the paddle or erratic behavior) were punished with a fifteen second "time-out" period. During this period, all electronic equipment was turned off and the paddle apparatus was removed from the tank. A total of 500 training trials were run during eleven sessions. Training for the positive stimulus tapes ended when the subject reached a criterion level of 96 per cent correct responses for a block of fifty trials. The negative stimulus training tape was presented to the subject following the completion of the positive stimulus training period. The signal was presented through the same apparatus utilized in the earlier training and the paddle remained in the tank for the duration of the tape. The subject was neither rewarded nor punished for his action. This exposure to the negative stimulus was merely a habituation process.

At this point, the experiment was carried out. As with the training trials, the test stimuli were presented underwater via the transducer and tape recorder system. The dolphin was required to press the paddle in response to a positive stimulus whistle and to swim randomly, without touching the paddle, in response to a negative stimulus whistle. Response time was limited to a ten second period and correct responses resulted in a fish reward. Incorrect responses (i.e., those in which the subject swam randomly

in response to a positive stimulus or pressed the paddle in response to a negative stimulus) resulted in a fifteen second "time-out" period during which time all equipment was turned off and the paddle box was removed from the water. The number of trials conducted on any given day varied according to weather conditions, the subject's attitude and the degree of subject satiation. Records were kept of all responses and associated behavior. Forty-six blocks, of fifty trials each, were run. The criterion level for the solution of the problem was set at 96 per cent correct responses within a block of trials.

As a control on the subject, the experimenter and the equipment, a second whistle discrimination problem was presented to the subject. This procedure involved a previously solved, simple whistle discrimination experiment (details of this procedure may be found in Caldwell, Caldwell & Hall, 1971). Tapes used in the original testing of this problem were again utilized and presented to the subject via the same apparatus used in the dialect discrimination task. The subject correctly solved the problem and reached criterion level (ten correct responses in sequence) within the first fifteen trials. The first one hundred trials of this experiment were completed with a result of 97 per cent

correct responses. Based on these results, the subject, the experimenter and the equipment were judged to be functioning properly.

CHAPTER III

RESULTS

In an attempt to identify possible whistle dialects in the Atlantic bottlenosed dolphin, recorded whistles were analyzed by means of a spectrographic and an "audio-visual" technique. The resulting data were further investigated on the basis of the following population classifications: age class, sex, area of origin, region of origin, animals of like sex from adjacent regions and within-region sex and age classes. The characteristic parameters, utilized in the computations, were examined in an attempt to ascertain if a single parameter, and/or series of parameters, could be consistently used to identify whistle dialects within the varied population classifications. Whistles of two groups of dolphins (those animals originating in the Atlantic and Gulf coastal areas of Florida) were utilized in a dialect discrimination experiment in which a dolphin subject was trained to act as a discriminator of whistle dialects. All data were subjected to discriminant analysis in order to determine correct identification levels within the dolphin population

classifications. As a by-product of this statistical technique, mean values were found for each of the parameters investigated within the categorical population groupings.

Basic Data for Populations Studied

A list of the mean values for all the parameters investigated for each of the major categorical groupings of dolphins is presented in Table 2. These values are provided in order that comparisons may be made between these data and those of other investigators. The mean whistle of an average dolphin can be said to have an onset frequency of 7.5 kHz with an overall low frequency of 5.3 kHz and a high frequency of 14.6 kHz. The amount of time necessary to produce the modulation between the low and the high frequencies is 0.30 seconds. Whistle duration is between 0.81 and 0.93 seconds with each loop having a duration of 0.50 to 0.54 seconds. The minimum whistle duration is 0.33 seconds and the maximum duration is 1.95 seconds. The mean number of loops per whistle for the average dolphin is 2.1 with a maximum of 4.4 loops.

Although the exact degree of signature whistle use per dolphin was not calculated, on the average, the signature whistle occupied more than 90 per cent of a dolphin's

Table 2. Mean Values for All Whistle Parameters Examined Within Dolphin Subpopulations

Conditions	Sample Size	Frequency at Onset (in kHz)	Low Frequency (in kHz)	High Frequency (in kHz)	Frequency Modulation (in kHz)	Parameters: Frequency Modulation in Time (in seconds)	Spectrogram Loop Duration (in seconds)	Spectrogram Whistle Duration (in seconds)	Audio-Visual Whistle Duration (in seconds)	Audio-Visual Loop Duration (in seconds)	Minimum Whistle Duration (in seconds)	Maximum Whistle Duration (in seconds)	Average Number of Loops	Maximum Number of Loops
All Animals	158	7.5	5.3	14.6	9.3	0.30	0.50	0.81	0.93	0.54	0.33	1.95	2.1	4.4
Atlantic	74	8.0	5.1	14.5	9.4	0.32	0.53	0.81	0.91	0.56	0.34	1.91	1.8	4.0
Gulf	84	7.1	5.5	14.7	9.2	0.27	0.46	0.81	0.96	0.52	0.32	1.99	2.3	4.8
Males	69	7.5	5.3	14.9	9.6	0.33	0.51	0.84	0.91	0.53	0.32	1.91	1.9	4.2
Females	87	7.5	5.3	14.4	9.1	0.28	0.48	0.80	0.96	0.55	0.34	1.99	2.2	4.6
Atlantic Male	29	8.0	5.2	14.3	9.1	0.36	0.55	0.83	0.91	0.58	0.38	1.82	1.8	3.8
Atl. Female	43	8.0	5.0	14.8	9.7	0.30	0.52	0.81	0.91	0.55	0.31	1.97	1.9	4.0
Gulf Male	40	7.2	5.4	15.4	9.9	0.30	0.48	0.84	0.91	0.50	0.27	1.97	2.0	4.5
Gulf Female	44	7.1	5.5	14.0	8.5	0.25	0.44	0.78	1.01	0.54	0.37	2.01	2.5	5.1
Age Group 1	48	8.0	5.4	15.1	9.7	0.36	0.57	0.84	0.90	0.59	0.34	1.79	1.8	3.5
Age Group 2	61	7.4	5.3	14.0	8.8	0.28	0.50	0.83	1.01	0.54	0.31	2.12	2.4	5.2
Age Group 3	46	7.1	5.2	14.8	9.6	0.25	0.41	0.78	0.89	0.49	0.34	1.92	2.0	4.4
St. Augustine	44	7.9	4.7	14.6	9.9	0.30	0.50	0.75	0.95	0.54	0.38	1.80	1.9	3.9
Melbourne	13	9.5	5.8	14.3	8.5	0.43	0.76	1.01	0.86	0.67	0.27	2.31	1.4	3.4
Keys	10	7.0	5.4	13.9	8.5	0.36	0.48	0.75	0.81	0.56	0.26	2.03	1.7	4.5
Tampa	22	6.5	6.1	15.3	9.1	0.32	0.59	0.85	0.93	0.61	0.33	2.01	1.7	4.2
Steinhatchee	32	7.2	4.8	14.4	9.6	0.25	0.43	0.82	1.10	0.52	0.38	2.09	2.9	5.9
Destin	25	7.4	5.7	14.6	8.9	0.29	0.42	0.77	0.83	0.47	0.22	1.83	1.9	3.9

whistle repertoire. Only one dolphin was found to use two signature whistles. Another animal appeared to utilize a large assortment of different whistle contour with no one signature whistle being predominant.

Age- and Sex-Related Whistle Differences

The combined whistle data was evaluated, using discriminant analysis, to detect the possible presence of sex-, age- and sex-age-related whistle differences. The results of these computations are presented in Table 3. As may be seen, the male and female dolphins were correctly classified at the 56.5 per cent and 55.2 per cent levels, respectively. Overall, 55.8 per cent of the dolphins were placed into their appropriate sex categories. The following levels of accurate classification were computed for the dolphin age classes: class 1 (juvenile) 52.1 per cent, class 2 (subadult) 42.6 per cent, and class 3 (adult) 50.0 per cent. The overall correct classification level for the age category was found to be 48.1 per cent.

The whistle parameter data of the sex-age classes were then subjected to a discriminant analysis technique. The results of these computations yielded the following levels of accurate identification: age class 1 males 28.6 per cent,

Table 3. Classification of Dolphins into Sex, Age and Sex-Age Groups Based Upon Differences in Whistle Parameter Data

Classification	Group	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
Sex	Male	69	39	56.5	55.8
	Female	87	48	55.2	
Age	Class 1	48	25	52.1	
	Class 2	61	26	42.6	48.1
	Class 3	46	23	50.0	
Sex-Age	Male Age Class 1	28	8	28.6	
	Male Age Class 2	28	13	46.4	
	Male Age Class 3	12	6	50.0	
	Female Age Class 1	20	13	65.0	42.9
	Female Age Class 2	33	11	33.3	
	Female Age Class 3	34	8	23.5	

age class 2 males 46.4 per cent, age class 3 males 50.0 per cent, age class 1 females 65.0 per cent, age class 2 females 33.3 per cent and age class 3 females 23.5 per cent. In the overall sex-age class results, 41.0 per cent of the males were grouped into the female category and 23.0 per cent of the females were incorrectly classed as males. A level of 42.9 per cent correct classification was calculated for all dolphins involved in the sex-age groupings. Although the results of this phase of the study offer little evidence of discriminatory differences in the whistles of dolphins in these population categories, it should be noted that the results are considerably higher than chance level for the sex-age category dolphin groups.

Atlantic Versus Gulf Dialect Comparisons

The whistles of dolphins originating from two major coastal areas of Florida (Atlantic and Gulf) were subjected to analyses in order to determine if any dialectical whistle differences exist between these two large populations. The results of these comparisons are listed in Table 4. As may be seen, the combined data exhibited correct classification levels of 55.4 per cent for the Atlantic area dolphins and

Table 4. Degree of Correct Classification of Dolphins Expressed Both in Number and in Per Cent into Regions of Origin Based Upon Whistle Parameter Data.

Condition	Area	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
Combined	Atlantic	74	41	55.4	
	Gulf	84	56	66.7	61.9
Combined (With limitations)	Atlantic	49	31	63.3	
	Gulf	56	34	60.7	61.9
Males	Atlantic	29	19	65.5	
	Gulf	40	27	67.5	66.7
Females	Atlantic	43	28	65.1	
	Gulf	44	28	63.6	64.4

66.7 per cent for the Gulf area dolphins. Overall, 61.9 per cent of the dolphins from the two areas were precisely identified. When the restrictions of using only Atlantic area dolphins from north of New Smyrna Beach and Gulf area dolphins from north of Homosassa Bay were imposed, the Atlantic area dolphins were accurately classified at a 63.3 per cent level while the Gulf area dolphins had a slightly lower level of 60.7 per cent. Under these constraints, 61.9 per cent of the dolphins were placed into their appropriate area classification.

Classification tables were computed in order to examine the possibility that only dolphins of a particular sex might be accurately identified as having originated in a specific coastal area. On this basis, it was found that 65.5 per cent of the Atlantic males and 67.5 per cent of the Gulf males were correctly classified. The degree of accurate identification was slightly lower for the respective female populations; with 65.1 per cent of the Atlantic females and 63.6 per cent of the Gulf females placed into their appropriate areas. Overall, 66.7 per cent of the males and 64.4 per cent of the females were accurately classed into their regions of origin.

Regional Dialects

The possibility was considered that dialects might exist in smaller regional areas due to isolation of populations. Whistle parameters of dolphins originating in regional groups, both geographically distant and adjacent, were analyzed, in order to determine the potential of ascribing dolphins to a particular regional origin via their whistle emissions. Further investigations were conducted to explore the possibility that dolphins of like sex, from adjacent regions, utilize whistle dialects. Whistle data from dolphins originating in the two regional groups with the largest sample sizes, St. Augustine and Steinhatchee, were examined to determine if any within-group sex-, age- or sex-age class-related discriminative whistle differences existed.

Geographically Distant Regions

The results of the ten non-adjacent regional group discriminations are listed in Table 5. The levels of correct identification for these regions ranged from 59.4-100.0 per cent, while a 69.3-97.2 per cent range can be seen for the overall groupings of these regions. The three highest levels of overall correct classifications correlated

Table 5. Classification of Dolphins from Geographically Distant Non-Adjacent Regions into Correct Regions of Origin Based upon Whistle Parameter Differences.

Discrimination	Region	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
St. Augustine vs. Keys	St. Augustine	44	37	84.1	81.9
	Keys	10	7	70.0	
St. Augustine vs. Tampa	St. Augustine	44	37	84.1	84.9
	Tampa	22	19	86.4	
St. Augustine vs. Steinhatchee	St. Augustine	44	33	75.0	69.3
	Steinhatchee	32	19	59.4	
St. Augustine vs. Destin	St. Augustine	44	33	75.0	75.4
	Destin	25	19	76.0	
Melbourne vs. Tampa	Melbourne	13	13	100.0	97.2
	Tampa	22	21	95.5	
Melbourne vs. Destin	Melbourne	13	11	84.6	89.6
	Destin	25	23	92.0	
Melbourne vs. Steinhatchee	Melbourne	13	11	84.6	86.7
	Steinhatchee	32	28	87.5	
Keys vs. Destin	Keys	10	7	70.0	71.4
	Destin	25	18	72.0	

Table 5 (Continued)

Discrimination	Region	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
Keys vs. Steinhatchee	Keys	10	8	80.0	80.9
	Steinhatchee	32	26	81.2	
Tampa vs. Destin	Tampa	22	18	81.8	85.2
	Destin	25	22	88.0	

Mean Per Cent Correct = 81.85

with the presence of the Melbourne regional group. An overall mean accurate identification level for all dolphins originating in non-adjacent regions was found to be 81.85 per cent.

Geographically Adjacent Regions

Five combinations of adjacent groups were examined to explore the possibility that whistle dialects were utilized between regional groups. The results of the statistical computations are presented in Table 6. Correct classification levels ranged from 65.6-92.3 per cent and the overall correct classification levels for groups ranged from 72.6-91.3 per cent. Dolphins from adjacent regions were found to be accurately classified into their regions of origin for 83.29 per cent of the cases.

All Regional Groups

A mean correct classification level of 82.30 per cent was calculated for all fifteen regional discriminations. The discriminant analysis technique was applied to the whistle data of animals from all six regions, within a single discrimination, in order to determine the probability of a

Table 6. Correct Classifications of Dolphins from Adjacent Regions into Their Appropriate Regions of Origin Based Upon Whistle Parameter Differences

Discrimination	Region	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
St. Augustine vs. Melbourne	St. Augustine	44	38	86.4	84.4
	Melbourne	13	10	76.9	
Melbourne vs. Keys	Melbourne	13	12	92.3	91.3
	Keys	10	9	90.0	
Keys vs. Tampa	Keys	10	8	80.0	84.5
	Tampa	22	19	86.4	
Tampa vs. Steinhatchee	Tampa	22	20	90.9	87.2
	Steinhatchee	32	27	84.4	
Steinhatchee vs. Destin	Steinhatchee	32	21	65.6	72.6
	Destin	25	20	80.0	

Mean Per Cent Correct - 83.29

dolphin being assigned to its appropriate region of origin. The following levels of correct classifications were found: Melbourne region 61.5 per cent, Keys region 60.0 per cent, Destin region 52.0 per cent, Tampa region 50.0 per cent, St. Augustine region 38.6 per cent and Steinhatchee region 37.5 per cent. An overall mean correct identification level of 45.9 per cent was calculated. This number represents the probability of correctly classifying a dolphin into its appropriate region of origin when presented with all six possibilities.

Sex Related Whistle Differences Between Adjacent Regions

The whistle parameter data for dolphins of like sex from adjacent regions was analyzed to determine if whistle dialects were utilized, to a greater degree, by only one sex. The results of these calculations are presented in Table 7. It was found that males from adjacent regions exhibited a mean accurate identification level of 98.9 per cent with ranges of 91.7-100.0 per cent for correct classification and 96.7-100.0 per cent for overall correct classifications for groups. Females from adjacent regions had a 92.1 per cent mean accurate identification level. The ranges for

Table 7. Percentage and Number of Dolphins of Like Sex from Adjacent Regions Correctly Classified into Appropriate Regions of Origin Based Upon Differences in Whistle Parameters.

Discrimination	Region-Sex Group	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
St. Augustine vs. Melbourne	St. Augustine Male	20	20	100.0	100.0
	Melbourne Males	4	4	100.0	
	St. Augustine Females	23	20	87.0	87.5
	Melbourne Females	9	8	88.9	
Melbourne vs. Keys	Melbourne Males	4	4	100.0	100.0
	Keys Males	3	3	100.0	
	Melbourne Females	9	9	100.0	100.0
	Keys Females	7	7	100.0	
Keys vs. Tampa	Keys Males	3	3	100.0	100.0
	Tampa Males	10	10	100.0	
	Keys Females	7	7	100.0	100.0
	Tampa Females	12	12	100.0	
Tampa vs. Steinhatchee	Tampa Males	10	10	100.0	100.0
	Steinhatchee Males	12	12	100.0	
	Tampa Females	12	11	91.7	90.6
	Steinhatchee Females	20	18	90.0	

Table 7 (Continued)

Discrimination	Region-Sex Group	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
Steinhatchee vs. Destin	Steinhatchee Males	12	11	91.7	
	Destin Males	17	17	100.0	96.7
	Steinhatchee Females	20	18	90.0	
	Destin Females	8	7	87.5	89.3

Mean Per Cent Correct - 95.34

female dolphins were 87.0-100.0 per cent for correct classification and 87.5-100.0 per cent for overall correct classifications for groups. An overall mean accurate identification level of 95.34 per cent was calculated for both sexes.

Investigations Within Regional Groups

The two regions with the largest populations (St. Augustine and Steinhatchee) were individually examined to detect the possible presence of sex-, age- and sex-age group whistle differences within each region. These computations were made in order to determine if sexually segregated herds and/or dominance hierarchies may be maintained by such whistle dissimilarities. The results of these calculations are presented in Table 8. Male dolphins from the St. Augustine region had an 80.0 per cent correct classification level and females of this region were correctly classified in 78.3 per cent of the cases. Overall, dolphins from this region were accurately placed into the appropriate sex category at the 79.1 per cent level. St. Augustine region dolphins displayed the following correct identification levels: age class 1 = 88.9 per cent, age class 2 = 77.8 per cent, age class 3 = 66.7 per cent. The overall accurate classification level

Table 8. The Within-Region Correct Classification Levels for St. Augustine Region and Steinhatchee Region Dolphins Expressed in Percentage and Number of Animals Classified into Their Appropriate Sex, Age and Sex-Age Groups.

Region	Classifiaction	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
St. Augustine	Male	20	16	80.0	
	Female	23	18	78.3	79.1
St. Augustine	Age Class 1	9	8	88.9	
	Age Class 2	18	14	77.8	77.1
	Age Class 3	15	10	66.7	
St. Augustine	Male Age Class 1	5	4	80.0	
	Male Age Class 2	9	7	77.8	79.4
	Male Age Class 3	5	4	80.0	
	Female Age Class 1	4	4	100.0	
	Female Age Class 2	9	7	77.8	
	Female Age Class 3	10	7	70.0	
Steinhatchee	Male	12	10	83.3	
	Female	20	16	80.0	81.3
Steinhatchee	Age Class 1	13	8	61.5	
	Age Class 2	13	8	61.5	72.0
	Age Class 3	6	6	100.0	
Steinhatchee	Male Age Class 1	7	5	71.4	
	Male Age Class 2	4	2	50.0	

Table 8 (Continued)

Region	Classification	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
	Male Age Class 3	1	1	100.0	
	Female Age Class 1	6	6	100.0	73.4
	Female Age Class 2	9	5	55.6	
	Female Age Class 3	5	3	60.0	

for St. Augustine region age classes was 77.1 per cent. The following correct classification levels were found for St. Augustine sex-age classes: class 1 males 80.0 per cent, class 2 males 77.8 per cent, class 3 males 80.0 per cent, class 1 females 100.0 per cent, class 2 females 77.8 per cent, and class 3 females 70.0 per cent. In the overall St. Augustine region sex-age class results, 15.8 per cent of the males were incorrectly classed as females and 13.0 per cent of the females were incorrectly classed as males. A correct identification level of 79.4 per cent was found for all the animals of this region for this category.

The Steinhatchee region male dolphins were correctly identified 83.3 per cent of the time and females of this region had an 80.0 per cent correct level. Overall, dolphins from this region were accurately classified into the appropriate sex at the 81.3 per cent level. Age classes of dolphins from this region exhibited the following correct classification levels: age class 1 = 61.5 per cent, age class 2 = 61.5 per cent and age class 3 = 100.0 per cent. Overall, dolphins from the Steinhatchee region were correctly placed into the appropriate age classes at the 72.0 per cent level. The following accurate identification levels were found for Steinhatchee sex-age classes; class 1 males 71.4

per cent, class 2 males 50.0 per cent, class 3 males 100.0 per cent; class 1 females 100.0 per cent, class 2 females 55.6 per cent and class 3 females 60.0 per cent. Males were incorrectly classed as females in 16.7 per cent of the cases and females were incorrectly classed as males in 20.0 per cent of the cases. A correct identification level of 73.4 per cent was found for all dolphins from this region for the sex-age class category.

Whistle Parameters Involved in Computations

Although the discriminant analysis procedure utilized in this project employs a stepwise method of computation, the resulting classification table can be said to be based upon a multiple set of best predictors. For example, none of the classification table results reported in this section were formed solely by the influence of a single whistle parameter. Likewise, no particular ordered set of whistle parameters was consistently employed in the computation of the classification tables. It was observed, however, that the parameter most often selected as having the highest potential for discriminating regional whistle differences was spectrogram loop duration. Again, it should be remembered that in no case was this parameter used as the sole discriminator.

Based upon a built-in tolerance test, certain parameters were excluded from computation; although, in this case also, no one parameter was consistently excluded. Usually one of the following three parameters was not employed in the computation; low frequency, high frequency and frequency modulation.

Dialect Discrimination Experiment

A dolphin subject was utilized in this experiment as a potential discriminator of dialectical whistle differences between dolphins originating in the Atlantic coastal area of Florida and those from the Gulf coastal area. Upon the completion of 2300 trials, the subject was judged unable to differentiate between the whistles of the dolphins from the two areas since he was unable to attain the predetermined criterion level of 96 per cent correct within a fifty trial session. Specifically, the overall level of subject achievement was 52.26 per cent correct classification. The percentage of correct responses versus the number of experimental sessions is plotted in Figure 3.

The whistles of the dolphins utilized in this experiment were analyzed and divided into component parameters on the same basis as the dolphin whistle parameters utilized in the previously described phases of this project. The resulting

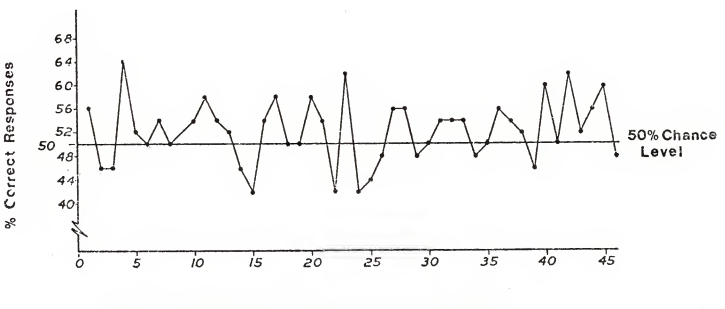


Figure 3. Percentage of Correct Responses Achieved by the Dolphin Subject Utilized in the Whistle Dialect Discrimination Experiment. The Correct Identification Levels Attained for Each Session of Fifty Trials Are Plotted.

parameters were then subjected to the discriminant analysis technique and the results are presented in Table 9. The Atlantic dolphins were correctly classified in 65.2 per cent of the cases and the Gulf dolphins had a 68.0 per cent correct identification level. Overall, the dolphins involved in this discrimination exhibited a 66.6 per cent level of correct classification.

Table 9. Percentage and Number of Dolphins Utilized in Dialect Discrimination Experiment That Were Correctly Classified into Appropriate Areas of Origin Based Upon Whistle Parameter Differences.

Area	Sample Size	Number Correctly Classified	Per Cent Correct	Overall Per Cent Correct for Groups
Atlantic	25	16	65.2	66.6
Gulf	25	17	68.0	

CHAPTER IV

DISCUSSION

Mean Whistle Parameters

The mean values for the whistle parameters, utilized in the various phases of this study, are reported in order to provide a basis of comparison with similar data published by other investigators. The values generated in this project are listed in Table 2 and are based upon a total sample size of 158 individual dolphins. Earlier workers in the field, however, have based their descriptions of these whistle parameters on sample sizes of usually less than ten animals. Thus, direct comparisons between the published values and those used in this study may prove to be somewhat difficult. Moreover, most earlier experimenters analyzed only a few of the parameters that are potentially measureable. Nevertheless, it was deemed important to attempt to compare the values in order to determine the degree of similarity among the various investigations.

Frequency at onset was one of the most often studied

parameters of the dolphin whistle; a mean value of 7.5 kHz was found for the animals (total population) studied in this research. This value was found to be relatively comparable to the onset frequencies found by other researchers, viz. 7 kHz (Kellogg, Kohler & Morris, 1953), 8-10 kHz (Evans & Prescott, 1962) and 4-8 kHz (Dreher, 1966). The mean low frequency of the whistle in the present study was found to be 5.3 kHz, a value slightly higher than those reported by Dreher (1961), 4 kHz; Lilly and Miller (1961a), 4 kHz; Evans and Prescott (1962), 3.7 kHz; Dreher and Evans (1964), 5 kHz. Further, the value of 14.6 kHz, which was computed for the mean high frequency, was comparable to those reported by Kellogg, Kohler and Morris (1953), 15 kHz; by Dreher and Evans (1964), 16 kHz; and by Dreher (1966) at 10-16 kHz but lower than the values reported by Evans and Prescott (1962) 20-22 kHz and Lilly and Miller (1961a) 18 kHz. The mean frequency modulations of 9.3 kHz, obtained for the dolphins in this study, was higher than the 8 kHz value reported by Kellogg, Kohler and Morris (1953) and by Kellogg (1961), but lower than the 11 kHz reported by Dreher (1961) and the 14 kHz and the 16 kHz values found by Lilly and Miller (1961a) and Evans and Prescott (1962), respectively.

Whistle duration was another of the parameters measured.

The values of 0.81 sec (via spectrographic analysis) and 0.93 sec (via "audio-visual" analysis) found for this parameter were larger than those reported by Lilly and Miller (1961a) 0.25 sec, by Kellogg, Kohler and Morris (1953) and by Dreher (1961), 0.50 sec. Sex and age variations appeared to account for only slight changes in whistle duration values, therefore, the large differences between the sample sizes examined were the probable cause of the slightly different results. None of the available literature offered any quantification of the other parameters investigated in this study. Overall, it appeared that the mean values found for the whistle parameters measured in this study were quite similar to those reported in the literature by earlier investigators.

It was of interest to note that the approximation of signature whistle use at over 90 per cent of the average dolphin's whistle repertoire lent support to the Caldwell hypothesis. They reported (Caldwell & Caldwell, 1968) that this type of phonation makes up at least 90 per cent and sometimes almost 100 per cent of an individual dolphin's whistles. Although two dolphins did vary in their use of signature whistle patterns, they represent only an insignificant number within the very large population studied.

Age- and Sex-Influenced Differences Within the Dolphin Population Studied

The whistle parameters for the total dolphin population were analyzed in an attempt to determine if intragroup whistle differences were present within the dolphin sex, age and sex-age subpopulations. Table 3 contains the results of these analyses. Since only 55.8 per cent of the dolphins were classified into their appropriate sex category, it appeared that little variation existed between the whistles of male and female Atlantic bottlenosed dolphins. This judgement is strengthened by Caldwell, Caldwell and Hall (1971) who demonstrated that the ability of a dolphin to discriminate between the whistles of conspecifics was not affected by the sex of the emitter.

With respect to age, the analyses of the whistle parameters of the total population yielded little positive evidence for the presence of discriminate whistle differences. The sex-age class data, however, exhibited a greater probability of utilizing whistles differences (re: chance levels) than did either the data for sex or age. However, it is difficult to ascribe any importance to the individual sex-age class results since the best results, for the males, were for age class three and the highest results for the females were in

age class one. A possible advantage of dolphins having the capacity to discriminate amongst sex-age groups would be the ability to locate sexually mature partners for mating purposes. If this relationship is accurate, it would be expected that the age class three (adult) dolphins of both sexes would possess the most easily distinguishable whistle differences. In this regard, Essapian (1953) noted that a particular female dolphin may respond to a bull's call. Another possible utilization of sex-age class whistle differences would be to maintain a dominance hierarchy within a dolphin herd. If only females and juveniles are present, the hierarchy appears to depend on size and age (Slijper, 1962). This dominance hierarchy even extends into captive dolphin herds and Tavolga (1966) was able to ascribe four subunits to such a structure. The first subunit was solely the adult male, who was the dominant animal in the tank. Adult females made up the second subunit, with the third being composed of subadults (the majority of which were males). As would be expected, juveniles of both sexes were in the fourth subunit. While it is apparent that a sex-age group discriminatory ability might have limited uses, the results of this study provided only slight evidence for the presence of sex-age class whistle differences in the Florida population of this species.

Atlantic Versus Gulf Area Dialect Comparisons

Since the analyses of the whistle parameters of the total dolphin population only suggested the existence of whistle dialects, the subjects were divided into smaller subpopulations (based on area of origin) in an effort to determine if there were dialects embodied in the overall group, i.e., in the subpopulations. As indicated by the results presented in Table 4, there appears to be no real indication that whistle dialects existed between dolphins from the two large sea areas adjacent to the Atlantic and Gulf coasts of Florida. Moreover, no improvement in the classification of the dolphins into their appropriate areas was noted even when animals originating in areas north of New Smyrna Beach on the Atlantic coast and north of Homassassa Bay on the Gulf coast were compared. However, since the observed migrations of this species in Florida demonstrate that they have a vertical range of only 50-100 miles (Caldwell & Caldwell, 1972a), it is possible that the areas examined were too large and that dialects may be utilized by dolphins in smaller regional areas.

When only male dolphins were compared, re: the Atlantic and Gulf areas, the results exhibited only a slightly better

level of correct identification than that found for the total population. Results similar to those found for the males were noted for the Atlantic females when they were compared to the Gulf counterparts. It appeared that no dialectical differences existed within the whistles of dolphins originating in the two areas investigated in this study.

Regional Dialects

Since there was little indication that dialects may be present in the whistles of dolphins residing in relatively small areas, it was decided that smaller subpopulations of this species should be identified and studied. Accordingly, whistles of dolphins originating in these regional subpopulations were subjected to analysis.

Geographically Distant Regions

When the characteristics of dolphin whistles from geographically distant regions were compared (see Table 5), some evidence of the utilization of dialects by this species was found. The overall means correct classification level of 81.85 per cent, while still not of sufficient strength to support any positive conclusions, was considerably higher

than the mean correct identification value of the area comparison (61.9%). It appeared that the whistles of the Melbourne region dolphins might be more easily distinguished from those of other groups than the whistles of dolphins from any other region. This postulation was based upon the finding that the three highest correct identification levels resulted from discriminations involving the whistles of animals from the Melbourne region.

Geographically Adjacent Regions

Only slightly more compelling evidence was found for the utilization of whistle dialects by dolphins originating in adjacent regions (Table 6) than was found between dolphins from geographically distant regions (Table 5). This finding suggests that the formation of whistle dialects in this species was a result of population isolation rather than interaction between adjacent populations. Similarly, the elephant seal, *Mirounga angustirostris*, was found to form pulse rate dialects based upon an isolation of populations (LeBoeuf & Petrinovich, 1974) and this same type of relationship may hold for the bottlenosed dolphin. Specifically, if whistle dialects were developed in this species (*T. truncatus*) as a discouragement to the intermixing of subpopulations--such as

Nottebohm (1969) theorized with respect to the development of dialects in avian species--the largest correct identification levels should have been exhibited between adjacent groups (rather than distant populations) because these groups had the greatest potential for intermixing. Such a relationship, obviously, was not substantiated by the results of this study. Rather it appeared that the noted whistle dialects were distributed in a mosaic pattern with each region developing its dialect independent from influences of neighboring populations.

In an attempt to demonstrate the potential of the utilized whistle parameters to function as indicators of regional origin (i.e., dialects), these data from all six regions, were statistically analyzed on a simultaneous basis. The results (as stated in Chapter III) demonstrated that the Melbourne region dolphin whistles were easiest to discriminate from those of other regional groups; i.e., they had the highest correct classification level (61.5%). Indeed, this finding strengthens the earlier reported high degree of distinguishability of Melbourne region dolphin whistle emissions. Moreover, it should be remembered that a correct classification within a six-way discrimination has a chance level of approximately 16.7 per cent. Since the lowest level of

accurate identification, amongst these regions, was 37.5 per cent (for the Steinhatchee region), the probability that regional whistle dialects exist was more than twice that of chance. In any case, the mean overall correct classification level for all fifteen regional discriminations was found to be 82.30 per cent--a level only slightly higher than that for adjacent dolphin groups (82.29%). Thus, this finding reinforced the hypothesis that any regional whistle dialects that existed were independent of the influences of neighboring populations. Since it appeared that the regional whistle dialects utilized by this species were products of the isolation of populations, it would seem appropriate to review the possible causes of this isolation.

Substantial discussion can be found in the research literature concerning the possible influence of water currents in delineating cetacean migratory routes and in the formation of boundaries to their movements (Uda, 1954; Norris, 1967 and Nasu, 1974). Although the patterns of Florida water currents were used in this research to help form regional populations of dolphins (see again Figures 1 and 2), it appears that significant seasonal variations in the current patterns exist (Jones, O'Brien and Hsueh, 1973). Thus, it is probable that the effects of currents as isolating mechanisms for

Atlantic bottlenosed dolphins are relatively minor and other reasons for the formation of dialects must be sought. For example, it can be argued that the regional populations of bottlenosed dolphins may be well adapted to local ecological habitats. In this regard, it has been found that dolphins orient themselves to areas of high food productivity (Evans, 1971). Further, while movements of most cetacean herds are closely related to the migrations of their food fish species (Norris, 1967), the bottlenosed dolphin is relatively plastic in food preference (Leatherwood, 1975). It thus appears obvious that these dolphins are capable of maintaining particular territories. Indeed, there has been considerable speculation that Atlantic bottlenosed dolphins do not migrate for any appreciable distances and maintain specific habitats throughout the year (Caldwell, 1955; Caldwell & Golley, 1965; Caldwell, Caldwell & Seibenaler, 1965; Irvine & Wells, 1972).

Perhaps of greater significance is the possibility that whistle dialects may also be utilized within subdivisions of the regions used in this study. For example, Caldwell and Caldwell (1972a) report that dolphins reside in microterritories within their general habitats. However, it was not possible at this time to conduct such investigations. This

inability was due to the lack of sufficiently large sample sizes of recorded dolphin whistles within each of the regions. It should be noted also that if the regions could have been better identified, a greater amount of evidence of dialects might have resulted.

Sex Differences Between Adjacent Regions

Since the highest probability of whistle dialect utilization was exhibited between adjacent regions, an attempt was made to further delineate the extent of such dialect use between these regions. Specifically, whistles of dolphins of like sex from adjacent regions were compared to determine if dialects occur as a function of sex, i.e., there may be a dialect indigenous to females only and another one for males only. The results of these discriminations (see again Table 7) showed an overall correct classification level of 98.9 per cent for males suggesting that whistle dialects may be sex-related. Further, although the female dolphins exhibited a slightly lower 92.1 per cent correct identification level, the same sex-related whistle dialect relationship appears likely.

The overall mean correct identification level for both sexes, from adjacent regions, was 95.34 per cent. Since

this level was higher than the level attained for the adjacent region discrimination (83.29%), it can be assumed that whistle dialects might exist for the Atlantic bottlenosed dolphin both as a function of region and sex. However, sample sizes were quite small when groups of dolphins of like sex from adjacent regions were studied. It also can be argued that the statistical technique used in this study may have had a built-in bias which decreased as population size increased. In research such as this, however, data on dolphin populations as large as that studied are rarely obtainable; thus, a decision was made to proceed with the analysis in spite of the relatively small number of animals in each group. This approach was utilized because the importance of finding relevant whistle dialect relationships outweighs the slight risk of drawing unrealistic conclusions.

Investigations Within Regional Groups

It has been demonstrated that whistle dialects probably exist between dolphins residing in different geographic regions. Further, it was felt that the degree of utilization of whistle differences within regions should be investigated. Harris and Lemon (1972) reported that, in all avian species

that utilize dialects, there are not only song differences between populations, but also greater or lesser amounts of song variations within a given population. A similar relationship may be true for dolphins. In order to test this assumption, the whistles of dolphins from the St. Augustine and Steinhatchee regions were chosen for investigation. Similar results were exhibited by both regions in regard to possible sex-related, within-region discriminative whistle differences. That is, the correct classification level found for the St. Augustine region was 79.1 per cent and 81.3 per cent was found for the Steinhatchee region. Thus it appears that some evidence exists for the utilization of sex-related whistle differences within regional populations.

The next relationship examined was the possible utilization of age-related whistle differences within regional populations. Age (class) correct identification levels for the two regions (77.1% for St. Augustine and 72.0% for Steinhatchee) were substantially higher than were the age levels for the overall dolphin population (48.1%). These results may reflect the presence of whistle differences capable of sorting dolphins into different age classes. Of course, it is possible that more or fewer age classes exist than those that were specified for this research and that each might exhibit

unique distinctions. This possible misclassification of age groups could explain the less than perfect classification levels found for the age classes. Nevertheless, evidence exists permitting the conclusion that age-related whistle differences may be utilized within regional groups of dolphins.

The overall group correct classification levels for sex-age groups within the two regions examined were 79.4 per cent for St. Augustine and 73.4 per cent for Steinhatchee. These levels were substantially higher than that found for the sex-age groups of the overall population (42.9%) and offer some indication of the presence of whistle differences within regional sex-age groups.

It is quite reasonable to assume that male dolphins possess discriminative whistle differences because it is often the males of a species that posses them (Marler & Tamura, 1964; LeBoeuf & Petrinovich, 1974). However, in the case of this research, females also appeared to exhibit such differences. It is also possible to explain the function of these relationships on the basis of sexual homogeneity within a group of bottlenosed dolphins (True, 1891; Mead, 1975). During mating seasons, this sexual homogeneity is apparently replaced by a mixing of the breeding animals. It appears reasonable that, in this case, it would be

advantageous for male and female dolphins within a region, to produce easily recognizable whistles to facilitate the location of potential breeding partners. The importance of such sex recognition was noted by Orejuela and Morton (1975) for an avian species; it also may hold for cetaceans. In any case, the requirement of optimal breeding success for a species could explain the presence of whistle differences within sex-age groups since not only must a breeding partner of the appropriate sex be found, but this individual must be of sufficient age for reproductive activity.

Thus, evidence exists for the utilization of whistle differences by Atlantic bottlenosed dolphins in Florida waters. An attempt was made to determine which particular whistle parameters were involved in the composition of dialects. In addition a captive dolphin was used as a "dialects discriminator."

Whistle Parameters Involved in Computations

As was pointed out in the results section, the discriminant analysis technique utilized in this study produces results based upon a multiple set of best predictors. It is the combined effects of variables that is of importance,

rather than the contribution of a single variable. Therefore, it is difficult to draw any conclusions regarding which individual parameters make up the whistle dialects. No single parameter was used to form the classification tables for any of the discriminations conducted in this study. Similarly, no particular set of variables aided in the computation of classification tables for all dolphin subpopulations examined. However, it can be concluded, from these data, that the larger the set of whistle parameter measurements, the higher the level of correct identification. This finding is quite similar to that of Busnel (1966) who reported that, in order to obtain a valid interpretation of an acoustic signal, one should use analysis methods which utilize as many parameters as possible. This technique accounts for the presence of a number of the minute structural details of the signal.

The fact that there was no consistent use of any particular parameter in the creation of the dialects appears to lend support to the theory that it was the isolation of populations that gave rise to dialect formation in this species. That is, if dialects had been developed to prevent the intermixing of adjacent populations, it should have been possible to identify consistently altered whistle parameters

between adjacent populations. All thirteen whistle parameters were involved in the discriminations of the adjacent regional areas. The order in which these variables were used in this stepwise procedure was different for each discrimination; no two were the same. Again, it would be incorrect to ascribe importance to a single parameter since the set of variables is used for discrimination. The frequency of utilization of the spectrogram loop duration as the best individual predictor of regional dialects gives only slight indication of the importance of this parameter. In none of the regional discrimination was this parameter the sole discriminator.

Even though no single parameter was consistently excluded from the data sets, three parameters often were rarely used in conjunction with one another. These parameters were low frequency, high frequency and frequency modulation. It appears that a possible reason for omission of the frequency modulation measurement would be that it duplicates the information offered by the other two parameters. Since the frequency modulation is defined as the difference (in kHz) between the low and high frequency extremes in a whistle, the low frequency or the high frequency measurement could be eliminated without any loss of acoustic information.

To summarize, in order to achieve the highest level of

correct classification of dolphins into their appropriate subpopulations, the largest available set of acoustic measurements should be utilized. It is the entire set of parameters, used in various sequences that is important in the computation of dialectical whistle differences.

Dialect Discrimination Experiment

It will be remembered that, as a further test of the presence of area-related whistle dialects in this species, a dolphin subject was trained to function as a whistle discriminator. The test stimuli were the whistles of dolphins from the Atlantic and Gulf coastal waters of Florida. It was found that the subject was unable to discriminate between the whistles of animals from these two areas; thus, dialectical differences probably did not exist within the population used in this study. Indeed, the correct identification level of 52.26 per cent achieved by the subject was little better than chance level. However, when the whistle parameter data obtained from the animals utilized in this experiment were statistically analyzed, a correct classification level of 66.6 per cent resulted (see again Table 9). While these results were somewhat better than those attained by the dolphin subject, neither can be said to be indicative of the presence of an area-related whistle

dialect for this species in Florida waters.

Unfortunately, this dialect experiment was completed before the "field" recordings were collected--and also prior to any statistical analyses of the whistle parameter data. Hence, no testing of regional whistle dialects could be conducted using this dolphin subject. It can be conjectured, however, that the subject would be able to discriminate between regional whistle dialects if proper training techniques were utilized. Finally, it should be remembered that a dolphin in the "wild" would only be able to discriminate regional dialects in terms of familiar or alien since the animal has had little exposure to any dialects other than the one utilized by his own herd and those of adjacent populations.

Conclusions

It is obvious from the results that the Atlantic bottlenosed dolphin (*Tursiops truncatus*), in Florida waters, utilizes whistle dialects. Sufficient evidence exists to justify the existence of sex, age and sex-age class whistle differences within certain subpopulations. Determinations of the extent of dialect use within this species could not be made due to the limited size of the population investigated.

Based on the results of the whistle analyses, the following conclusions were formulated:

1. There appear to be no area-related (i.e., Atlantic coastal waters vs. Gulf coastal waters) dialects in the whistles of the dolphins originating in these locations. This condition can be substantiated by the results of the dolphin dialect discrimination experiment.

2. There is a strong indication that regional whistle dialects are used by Tursiops truncatus who reside in Florida waters. These dialects, however, appear to be due to the isolation of ecologically well-adapted populations of dolphins. Each regional population probably develops its dialect independent of any influence from neighboring populations.

3. Whistle dialects found between dolphin populations in adjacent regions appear to be sex-related (i.e., males and females of a particular region utilize whistle dialects differing from their counterparts residing in adjacent regions.).

4. Some evidence exists for the presence of sex, age, and sex-age class whistle differences within regional groups. The probable function of these differences is to unite sexually mature breeding partners of the appropriate sexes and to maintain a dominance hierarchy.

5. It can be concluded that no single parameter or particular set of parameters was consistently used in the discrimination of whistle dialects. Hence, it is necessary to use a large multiple set of whistle parameters to achieve an accurate discrimination of dolphins by means of their respective dialects.

6. When the total dolphin population, utilized in this study, was investigated, no evidence was found for the presence of sex- or age-related whistle differences. However, there was some slight indication of sex-age class whistle differences being present within this population.

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BIOGRAPHICAL SKETCH

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Harry Hollien, Chairman
Professor of Speech

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